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Anhydrobiosis and programmed cell death in plants: Commonalities and Differences

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ABSTRACT

Anhydrobiosis is an adaptive strategy of certain organisms or specialised propagules to survive in the absence of water while programmed cell death (PCD) is a finely tuned cellular process of the selective elimination of targeted cell during developmental programme and perturbed biotic and abiotic conditions. Particularly during water stress both the strategies serve single purpose *i.e.*, survival indicating PCD may also function as an adaptive process under certain conditions. During stress conditions PCD cause targeted cells death in order to keep the homeostatic balance required for the organism survival, whereas anhydrobiosis suspends cellular metabolic functions mimicking a state similar to death until reestablishment of the favourable conditions. Anhydrobiosis is commonly observed among organisms that have ability to revive their metabolism on rehydration after removal of all or almost all cellular water without damage. This feature is widely represented in terrestrial cyanobacteria and bryophytes where it is very common in both vegetative and reproductive stages of life-cycle. In the course of evolution, with the development of advanced vascular system in higher plants, anhydrobiosis was gradually lost from the vegetative phase of life-cycle. Though it is retained in resurrection plants that primarily belong to thallophytes and a small group of vascular angiosperm, it can be mostly found restricted in orthodox seeds of higher plants. On the contrary, PCD is a common process in all eukaryotes from unicellular to multicellular organisms including higher plants and mammals. In this review we discuss physiological and biochemical commonalities and differences between anhydrobiosis and PCD.

Contents

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1. Introduction

Life forms on earth encompass a wide diversity that inhabits different climatic regions, ranging from cold ice caps to the hot springs and dry environment (*e.g.*, rocks, dessert) to wet ones (*e.g.*, ponds, lakes) in different geographical regions. This diversity reflects the adaptability of inhabitants at physiological, biochemical and genetic levels to cope with the prevailing environment. Occupying extreme environmental niche, certain organisms can survive removal of almost all of their cellular water without irreversible damage; such organisms are referred to as desiccation tolerant or anhydrobiotes [1–4] and the phenomenon itself as anhydrobiosis. Measurements of water potential by Gaff group indicated that even when plants are equilibrated at 50% relative humidity at 28 °C, they experience a water deficit equivalent to that of −100 MPa pressure which is lethal for the majority of angiosperms [5]. Desiccation or drought tolerant organisms on the other hand have the ability to survive dehydration, to the point where moisture content in the cytoplasm has no free water, *i.e.*, ∼0.3 g H_2O/g dry weight, a condition where most of the cellular water is bound with macro-molecules. Resumption of normal life after rehydration is a significant feature of desiccation tolerance [6].

In contrast to anhydrobiosis, programmed cell death (PCD) ubiquitously occurs throughout all eukaryotic lineages. Though a regulatory process, PCD also act as one of the survival mechanisms *in planta* during certain instances of biotic and abiotic stresses such as disease, water stress, salt and heat stress [7]. PCD generally involves targeted killing of unwanted or diseased cells and is used to control cell number in the given tissue, thus maintaining homeostasis. Additionally, PCD is also observed during certain developmental processes as well where defined cells die and the dead cells take over their assigned function such as tracheary cells, sclerenchyma fibres and cork cells *in planta* [8]. Considering sensitivity of all the major crop plants to drought, understanding the process of anhydrobiosis and that of PCD has the potential to open up the possibility of introducing the drought resistance character in crop plants which could solve the global food security problem.

Anhydrobiosis is more prevalent in lower plants, especially in thallophytes, although involvement of anhydrobiosis in higher plants is not ruled out, the phenomenon is mostly restricted to some reproductive propagules like seeds. During evolution, with the development of water conducting system in higher plants PCD became one of the prominent strategies for the cellular homeostasis while anhydrobiosis progressively became restricted to certain reproductive structures as a mechanism to tide over the water stress conditions such as unfavourable dry weather or dissemination of propagules over longer distances where they were prone to be exposed to low water availability. There are certain species that manifest both the survival strategies. The higher plants bearing orthodox seeds are the ideal examples – manifesting both phenomena at successive developmental stages, *i.e.*, anhydrobiosis and PCD in the endosperm during seed maturation phase, while PCD in aleurone layer cells during seed germination. Existence of such examples in nature opens up the possibility of incorporating features to regulate PCD and promote vegetative desiccation tolerance at least up to certain extent in crop plants that lack this faculty.

In this review we have attempted to show that anhydrobiosis as well as PCD are survival strategies that have evolved independently in plants as a means of adaptation to their frequently changing environment. We have endeavoured to sketch a parallelism between these two processes and highlight a possibility to explore the phenomenon of anhydrobiosis for the acquisition of desiccation-tolerance in higher crop plants.

2. Origin and evolution of desiccation tolerance and programmed cell death (PCD)

Desiccation tolerance is a primitive trait that evolved when organisms originated in water took over terrestrial habitats [9–11]. Migration to land exposed the organisms primarily adapted to aquatic life-style to frequent desiccations due to heat, sunlight and wind. Thus, in order to thrive (*i.e.*, colonize and survive) in terrestrial habitat, aquatic plants acquired tolerance for dry conditions [12]. As the primitive architecture of early aquatic plants could not prevent the water loss on exposure to the frequent drying, the early land invaders developed intrinsic mechanisms that resisted harsh and frequent fluctuations in terrestrial environment. For example, desiccation tolerant lichens and bryophytes have ability to rehydrate within 15 min, resume net photosynthesis in less than an hour and resume full photosynthetic functions in about 24 h [13–15]. Apparently, to survive desiccation, the early plants (*e.g.*, bryophytes and lichens) would have acquired the ability to dehydrate slowly and rehydrate quickly. The acquisition of the slow dehydration characteristics during low water condition could have been the key to successful development of desiccation tolerance as exemplified by an aquatic moss *Fontinalis* where slow dehydration protected cells against desiccation induced damages through reduced production of ROS and oxidative bursts [16]. Most of the early land plants were tolerant to desiccation in their vegetative, as well as reproductive phase of life, but the loss of desiccation tolerance in vegetative phase of higher plants occurred during evolution of water transport system, such as tracheid and xylem vessels [10]. Programmed cell death (PCD) is also a trait which is believed to have originated and evolved with the origin of the first cell [17]. Although supposed to be diverse in nature with respect to means, executioners and phenotypes, PCD invariably functions as a regulated cell death as a means to make other members fitter to survive in a given environment. In case of unicellular organism the display of PCD is generally 'altruistic' in nature to help other members of the colony survive in limiting growth conditions (light, nutrients). In bacteria PCD acts as interesting toxin/antitoxin 'addiction modules' to attain a kind of enforced symbiosis, where their disruption could result in death of 'host cell'. The functions of PCD in multicellular organisms has evolved and elaborated further to involve/control the development and tissue homeostasis including protection from the diseases. These aspects have been comprehensively reviewed elsewhere [17]. Although origin of PCD could have been the culmination of multiple processes/mechanisms, in its simplest form it could be summed as the result of unavoidable stochastic 'self-destruct' tendency of most of the cell effectors/processes when their activity is beyond the control of cell survival factors as beautifully put forward by 'original sin' hypothesis [17].

3. Distribution of anhydrobiosis and PCD in photosynthetic organisms

Desiccation tolerance is observed in a wide range of taxa, including bacteria, algae and higher plants [18–23]. It is a primitive trait

and represented in cyanobacteria, bryophytes and pteridophytes, in both vegetative and reproductive structures, whereas in higher plants it is mostly restricted to the orthodox seeds and resurrection plants [9].

Cyanobacteria (blue green algae) represent a class of prokaryotes with photosynthetic activity and ability to mobilize atmospheric nitrogen through N_2 fixation. They are distributed in a range of environmental settings such as deserts, hot springs, ice caps [24]. A specimen of *Nostoc commune* – a terrestrial cyanobacterium, which was stored in desiccated state for more than 100 years, retained its ability to grow on rehydration [25,26]. In tropical and sub-tropical countries, blackish brown patches of cyanobacteria are very common on the surfaces of old buildings and bark of trees [19,27,28]. These cyanobacteria have been reported to survive extreme desiccation along with surface temperature which sometimes reaches up to 68 °C during summer season.

Among thallophytes – the most primitive plants, lichens and bryophytes have unique ability to survive from months up to years in the desiccated state. Anhydrobiosis is very common among thallophyta which are capable of restoring photosynthesis process within 15 min to 1 h after rehydration [29–32]. The desiccation tolerance at vegetative level is also typical for pteridophytes [33] but it is mostly lost in the higher plants, where it can be found primarily restricted to orthodox seeds and pollen [34]. Although sporadically represented, desiccation-tolerant vascular plants have been reported in 13 families belonging to monocots and ferns. Only few desiccation-tolerant dicots exist, and all are distributed among families *Gesneriaceae*, *Myrothamnaceae* and *Scrophulariaceae*. Altogether, about 330 species of vascular plants are known to show vegetative desiccation tolerance [35].

Contrary to anhydrobiosis, the PCD has been reported in all organisms evaluated to date from taxa belonging to groups of bacteria, algae and higher plants [36]. It is a trait displayed in both vegetative and reproductive structures suggesting its key role in growth, development and survival.

4. Mechanisms of desiccation tolerance

4.1. Cellular water and desiccation tolerance

The anhydrobiotic organisms suspend almost all metabolic activities during desiccation without irreversible damage, indicating that anhydrobiotic adaptations act at the membrane and macromolecular levels [37]. Studies on desiccation-tolerance of sub-aerial cyanobacterium *Scytonema geitleri* [21,22], showed that when dried microbial mats were allowed to take up water from environment or rehydrate, the water molecules show degree of preference for specific binding sites on macromolecules. The binding usually starts with charged regions or ionic sites followed by hydrogen binding and Van-der Waal's interaction sites. The number of strong binding sites directly correlated with desiccation tolerance. When analyzed for the resumption of physiological activities, energy generating reactions like photochemical reactions of photosynthesis resumed first, followed by increase in ATP level. At a later stage of hydration, the energy consuming activities, such as carbon and nitrogen fixation resumed [22]. During dehydration, the sequence of rehydration steps/reactions are followed in reverse order. This observation indicates that anhydrobiotic organisms have the ability to programme both suspension as well as resumption of physiological processes to withstand dehydration and resume life at the onset of favourable conditions.

The survival at extreme desiccation is a direct reflection of the capacity to retain water and its slow release during the period of desiccation. In most of the cyanobacteria shown to be desiccation tolerant, there is a slime layer on the surface of cells composed of exo-polysaccharides that reduce the cellular water loss during dehydration [38]. In some cyanobacterial species like *Gloeothece ATCC 27152*, water content of polysaccharides has been reported to be even higher than that of a cell interior [39]. Formation of spores (akinetes) in cyanobacteria is also purported to be part of the survival mechanism that protects it against the extreme environmental conditions such as desiccation. Interestingly, several desiccation tolerant filamentous cyanobacteria such as *Scytonema*, *Calothrix*, and *Lyngbya*, do not form spores [40], consistent with the fact that during evolution organisms would have evolved and perfected different strategies to achieve anhydrobiosis and desiccation tolerance to tide over water-limiting conditions regularly encountered in terrestrial habitats.

Cytological investigations made in desiccation tolerant moss *Physcomitrella patens* revealed that desiccation resulted into appearance of several small vesicles which were generated due to breakage of central large vacuole, denser cytoplasm and remarkable shrinkage of cell without the loss of plasma membrane integrity [41]. Changes in the shape of chloroplasts from ellipsoidal to spherical and disappearance of starch grains from chloroplasts have been also observed. Interestingly except vacuole and chloroplasts other sub-cellular organelles were not much disrupted [41]. Most of the cytological changes have been reported to prevent plasmolysis during desiccation [42]. The cytological changes in chloroplast have been argued as a meticulously developed protection strategy by anhydrobiotic organisms to facilitate their survival in desiccated state [41].

During evolution, when the early plants, *i.e.*, mosses and ferns, started to colonize the terrestrial habitats, some of them would have speciated and acquired evolutionary adaptations that ensured their survival in terrestrial habitats experiencing drastic changes in water potential such as development of conducting vessels with thick cell walls, presence of cuticle or waxy layer on epidermis, modifications that are directly involved in curtailing water loss from the cell, and development of strategies to minimize dependence on water for sexual reproduction and seed dispersal as observed in modern terrestrial plants [43]

4.2. Reactive oxygen species (ROS) and desiccation tolerance

ROS produced during cellular metabolism are responsible for the most of the damage to lipids, proteins and nucleic acids [44,45]. It is particularly destructive during desiccation of the photosynthetic tissues when carbon fixation is reduced as a result of water limiting conditions but the chlorophyll retains its ability to transfer electron after photo-excitation. Under such conditions, there is a continuous flow of electrons from photo-excited chlorophyll pigments to the ground state oxygen ($^3O_2$), which generates singlet oxygen ($^1O_2$) species. In addition, there is continuous generation of superoxide (O^{2-}), hydrogen peroxides (H_2O_2) and the highly toxic hydroxyl radical (*OH) from photosystem II [46]. Plants have developed several protective mechanisms to reduce ROS accumulation/generation, such as dissipation of excess energy *via* non-photochemical quenching (NPQ) by xanthophyll cycle [47], induction of antioxidants production (*e.g.*, ascorbate, tocopherol and glutathione) and increased production of ROS-detoxifying enzymes (*e.g.*, catalases, superoxide dismutase and peroxidases) [48,49]. As a protective mechanism, the cells of a desiccation tolerant cyanobacterium *N. commune* were shown to deactivate their photosynthetic systems activity on sensing water loss, and recover the photosystems I and II once favourable conditions return *i.e.*, rehydration [50]. Additionally, as indicated above the anhydrobiotic organisms have also developed elaborate mechanisms to orchestrate slow dehydration during desiccation to effectively reduce the generation of cellular ROS and suppress the oxidative

burst to reduce cellular damage during the process [16]. In order to protect cellular compartments from photo-oxidative damage during dry period, desiccation tolerant photoautotrophs have instituted mechanisms for the conservation and dissipation of light energy in photosynthesis by two different mechanisms. In one strategy energy dissipation in the antenna of photosystem (PS) II is facilitated. The rate of dissipation is even faster than energy capture process by the active reaction centre. In such scenarios where this photoprotection mechanism is insufficient, a second mechanism may become operational wherein energy dissipation is permitted in the reaction centre itself [51].

ROS mediated protein carbonylation is a type of modification suggested as one of the indicators of plant vigour under stressful conditions [52,53]. In a recent report on recalcitrant seeds of *Antiaris toxicaria*, the pretreatment of seeds with NO was found to overcome the inhibitory effect of desiccation and allowed the seeds to germinate. This inhibitory effect of desiccation on seed germination has been explained as increase in the activity of antioxidant ascorbate–glutathione pathway enzymes and metabolites on NO pretreatment which in turn diminished H_2O_2 production. This observation indicates a possibility of cross talk between ROS and Reactive Nitrogen Species (RNS) in the acquisition of adaptation during severe water scarcity [53,54]

4.3. Metabolic changes and desiccation tolerance

During the period of dehydration, anhydrobiotic organism undergoes metabolic changes particularly associated with sugar metabolism and/or synthesis of stress specific proteins [55]. These changes are thought to be brought about to provide protection to cellular membranes, macro-molecules and maintain structural integrity in the desiccated state of organisms. One of the widely employed strategy to survive desiccation involves overproduction of osmolytes, *e.g.*, trehalose, sucrose, myo-inositol, fructans, amino acids (proline), quaternary ammonium compound (glycine betain), polyols (*e.g.*, sorbitol, mannitol and D-pinnitol) that protect cellular membranes and macro-molecules in low water conditions [56]. Trehalose has been suggested to replace structural water of membrane and macromolecules, thus protecting its structural integrity [37,57,58] in low water conditions. Upon rehydration, water replaces osmolytes/osmoprotectants and the cells recover without damage. In extreme desiccation of anhydrobiotic cells, formation of a biologically inert glossy layer of osmolytes (vitrification) that acts as an inert protective matrix for the cells had been reported [59–62]. The osmoprotectant sugars were shown to interact with polar head groups of lipid membranes, keeping them liquid under drought conditions. Vitrification is also essential for protecting adjacent cell membrane bilayers from fusion to avoid/minimize the desiccation induced cell damage [37].

The elucidation of the molecular mechanism of the regulation of desiccation tolerance has highlighted the importance of inherently disordered hydrophilic proteins (IDPs), such as Late Embryogenesis Abundant (LEA) proteins, in the plant anhydrobiosis. Members of the LEA proteins are ubiquitous across the plant kingdom. LEA proteins are unstructured in solution and rich in glycine that amounts almost 6% of the total amino acid pool and have hydrophilicity index greater than 1 [63]. As the name suggests LEA are generally expressed during late stage of embryogenesis, *i.e.*, seed maturation, and in vegetative organs during exposure to water deficit condition. Ectopic expression of LEA has been shown to confer desiccation tolerance to a number of plants while absence of LEA has been shown to make them osmo-sensitive [64]. There are evidences suggesting that LEA proteins during water loss could help protect other proteins from aggregation [65–68], stabilize membranes, bind to DNA, bind to a variety of metal ions – effectively protecting the cells against ROS [66,69,70].

The repertoire of functions that IDPs may perform in cells has kept expanding. For example, the study of expression of another IDP named 'Anhydrin' in anhydrobiotic nematode *Aphelenchus avenae* has shown to make cells tolerant to desiccation-induced cell-damage by inhibition of the intracellular proteins' aggregation by acting as a chaperone [71]. Interestingly, 'anhydrin' was found to be able to act as 'endonuclease' that may act on supercoiled, linear, as well as chromatin linker DNA. This endonuclease function of 'anhydrin' is hypothesized to have a role in the repair of the desiccation-induced DNA damage or alternatively take part in the process of apoptosis or necrosis. Since, IDP members are scantly studied in general including that from plants, their overall role in the process of anhydrobiosis and the possibility of them playing a role in the execution of the PCD process is largely unexplored. Thus, there remains a distinct possibility that IDPs may have a role in both the processes.

5. Programmed cell death (PCD) in plants: its representation across kingdoms

PCD is a process that occurs in all eukaryotic organisms to sacrifice targeted cells in order to control cell number and remove unwanted or damaged cells, thus maintaining cellular homeostasis [72–74]. *In Planta*, PCD modulates several developmental and physiological processes like embryogenesis, xylem development, flowering and senescence [75–78]. Apart from regulating developmental programmes, PCD has been reported to play important role during biotic and environmental interactions ([79] and references therein). PCD can be induced *via* extrinsic pathway wherein the signal is perceived by membrane receptor or intrinsic pathway wherein it is triggered by release of pro-apoptotic proteins from mitochondria. In Plants, many of the executioners involved in animal apoptosis have not been identified yet. Some of features, which plants share with animal apoptosis, include cell shrinkage, chromatin condensation, and DNA fragmentation, release of cytochrome c from mitochondria and retention of some genes involved in autophagy. Differences include absence of classical caspases and formation of apoptotic bodies [80].

PCD has been reported from all kingdoms of life. It has been reported in a number of bacterium and slime moulds as well. Best studied example of bacterial PCD is toxin–antitoxin module (mazEF) located on bacterial chromosomes [81–83]. In slime moulds such as *Dictyostelium discoideum* that spend most of their lives as unicellular amoebae, during starvation the individual cells aggregate into a distinct 'slug' and form a fungus like structure consisting of both a stalk and spores. The spores from the fruiting structure disperse for a better hospitable environment, whereas the stalk cells undergo PCD [84,85]. Among algae, PCD has been reported from a number of species. Some well studied examples include *Dunaliella tertiolecta* during light deprivation [86], *Micrasterias denticulate* upon H_2O_2 induction [87], *Chlamydomonas reinhardtii* following UV radiation [88], *Chlorella saccharophila* during heat stress [89] and *Peridinium gatunense* in response to nutrient and light limitation [90]. PCD has been also studied in the budding yeast *Saccharomyces cerevisiae*, leading to the discovery of metacaspases in execution of PCD (Madeo et al., 2009). Lately, metacaspases have been also shown to play an important function in the execution of PCD in *Arabidopsis thaliana* [91,92].

The PCD mechanism in bryophytes is similar to those found in flowering plants. It is characterized by accumulation of ROS, induction of defence-related genes, such as *PAL*, *LOX*, *CHS* and *PR-1*, and activation of programmed cell death [93]. Interestingly, in mosses and ferns the neck canal cells lying above oogonium undergo coordinated autolysis process [94]. In gymnosperm seed, usually multiple embryos are formed, but due to competition for

the nutritional resources most embryos undergo PCD, except one embryo that survives and represents second generation [95]. In Norway spruce (*Picea abies*), there are two successive waves of PCD during somatic embryogenesis: the first wave is responsible for degradation of the most of the proembryogenic mass of cells that give rise to embryos, while the second wave eliminates terminally differentiated embryo-suspensor cells [96]. PCD in this system also requires activation of type II metacaspase mcII-Pa [97]. Additionally, the PCD also plays an important role in other developmental processes of higher plants, such as seed maturation and germination [76,98,99], xylem differentiation [78,100–103], leaf and organ senescence [77,104,105]. Plants also activate PCD in response to various environmental cues and during biotic interactions. Nonetheless, in contrast to animal apoptosis, the plant PCD remains poorly characterized [106].

6. Commonality and differences between anhydrobiosis and PCD, based on their function

Although PCD and anhydrobiosis are independent mechanisms that were adopted by plants during evolution, they share a common purpose that is survival during adverse conditions. Anhydrobiosis is supposed to primarily function as survival mechanism during desiccation, while PCD is supposed to act as a mechanism of cell elimination during different developmental stages and in biotic and abiotic stresses.

Some shared hallmarks and key executioners with their role in both PCD and anhydrobiosis of plants are described below. Cytological observations indicate that during both anhydrobiosis and PCD process while a dramatic shrinkage in cell size is observed, the integrity of plasma membrane is maintained [41,107]. In desiccated cells, central large vacuole breaks down into several vesicles while during PCD the vacuole becomes enlarged occupying almost all cellular volume and the sub-cellular components are pushed outside towards periphery. Nucleus remains intact with a block of condensed chromatin during anhydrobiosis while cells undergoing PCD initially display polylobal nucleus with chromatin condensation that later falls apart [31,32,41]. While minimal ultra-structural modifications have been reported in chloroplast and mitochondria during progressive desiccation of cells except appearance of spherical chloroplasts with a loss of starch granules and appearance of plastoglobuli, cells during PCD display swelled mitochondria and normal chloroplast that has lost the membrane integrity [31,32,41].

Although the studies unravelling the details of the molecular mechanisms and executioners of PCD that may be involved in anhydrobiosis as well remains scanty, some interesting details have emerged about this connection from the studies of Boris et al. [108]. The study had tried to identify the set of genes that may positively affect the survival of *S. cerevisiae* using single gene null mutant collection from EUROSCARF on rehydration following dehydration. Interestingly, the genes that encoded mitochondrial components of the cell death machinery, *i.e.*, apoptosis-inducing factor or *AIF* [109], *NUC1*-the major mitochondrial nuclease that has RNAse and DNA endo- and exonucleolytic activities [110], *CPR3* – a yeast homologue of cyclophilin D [111] and *QCR7* – a protein essential to respiratory activity [112,113], were found to negatively affect the anhydrobiosis or revival on rehydration. Although these PCD executioners were shown to definitely have a role in anhydrobiosis their exact role and molecular mechanism of action needs to be further elucidated as preliminary investigation entails previously unknown mechanism of action or functions. For example, the QCR7 appeared to enhance the death of cells following anhydrobiosis in a manner independent of the respiratory capacity, quite opposite to its well established respiratory capacity dependenct role in PCD.

7. Common regulators of programmed cell death and anhydrobiosis

7.1. Abscisic acid

Anhydrobiosis has been shown to be regulated in a number of plants by plant hormone abscisic acid (ABA) that functions in desiccation tolerance through modulation of the expression of genes involved in seed maturation [114–118]. In desiccation tolerant callus of resurrection plant *Craterostigma plantagenium*, ABA induced expression of a major gene involved in a stress signalling pathway named *Craterostigma desiccation tolerance* (*CDT-1*) [119]. A similar ABA-dependent pathway has been found in non-seed plants like algae and mosses such as *P. patens* [120,121]. One of the three homologues of the ABA transcription regulator '*ABA insensitive 3* (*ABI3*) found in *P. patens* had been shown to partially complement the *Arabidopsis abi3-6* mutant [122]; indicating that ABA-induced protection against desiccation is a conserved mechanism across plant kingdom. In a recent report, accumulation of ABA triggered by β-Aminobeuteric acid (BABA) treatment has been shown to act as non-hydraulic root signal resulting in stomatal closure, reduction in ROS production and higher anti-oxidant defence enzymes thus increasing the desiccation-tolerance in wheat cultivar [123].

Interestingly ABA has been reported to down regulate PCD in barley aleurone cells [124] and promote senescence in *Arabidopsis* [125]. In barley aleurone cells, Gibberelic acid (GA) induces PCD while ABA inhibits the process [126]. Furthermore, the ectopic expression of an ABA-induced protein HVA22 in aleurone cells had been found to inhibit the formation of large lytic vacuole, a characteristic feature of GA-induced PCD [126]. In Iris petals, ABA acts as a modulator of the senescence process in ethylene independent manner. In this system ABA activates protein phosphatase 2C (PP2C) which then regulates the downstream components essential for the cell death through dephosphorylation of an interacting component essential for ABA signalling [127].

7.2. Polyamines

Polyamines (PAs) are low molecular weight polycationic compounds involved in the regulation of various growth and developmental processes and their metabolism is shown to alter during various environmental cues such as chilling, drought, osmotic stress and salinity [128]. Due to polycationic nature, polyamines have strong ability to bind the negatively charged molecules like DNA, protein and membrane phospholipids [129], enabling cells the capacity to withstand stress induced damage. Polyamines are shown to be involved in desiccation tolerance. A study comparing mosses *Pseudevernia furfuracea* and *Ramalina farinacea* that display different extent of desiccation tolerance has underlined the key role of polyamines in conferring differential desiccation tolerance [130]. Moreover this report also indicated that polyamines modulate desiccation tolerance in combination of ABA indicating a positive regulator role of polyamines in anhydrobiosis. On contrary, PAs have been reported to modulate PCD through their metabolic derivatives [131]. The indication for the protective role of Polyamines in inhibiting PCD comes from a number of studies. A study by Papadakis and Roubelakis-Angelakis [132], showed that polyamines inhibit NADPH oxidase mediated super-oxide generation while a diamine named 'Puetrescine' inhibited PCD by attenuating the generation of H_2O_2 by polyamine catabolism *via* polyamine oxidases or PAOs. This study indicated that polyamines have the ability to reduce cellular ROS level which is required for the inhibition of ROS mediated PCD [132,132]. This is further supported by another report wherein polyamine catabolism by PAO had been demonstrated to be one of the key elements of oxidative burst which induces PCD in tobacco cells [133]. A link between

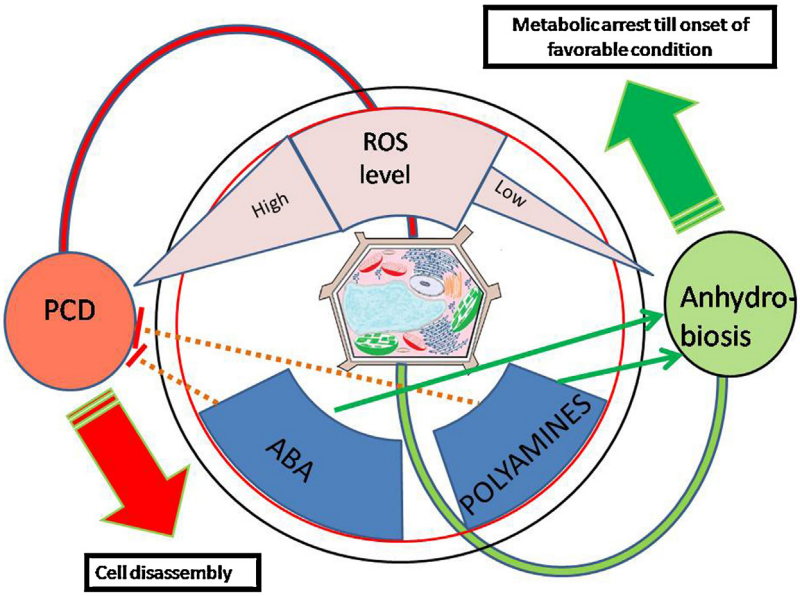

Fig. 1. Common regulators of anhydrobiosis and PCD. Anhydrobiosis and PCD are governed by ABA and polyamines. Higher level of cellular ROS (oxidative burst) is required for the stress induced PCD whereas low level of cellular ROS is required for Anhydrobiosis. Generally, ABA and Polyamines negatively regulate PCD but promote anhydrobiosis. Interplay of both positive and negative regulators of PCD and anhydrobiosis (*e.g.*, ABA and polyamines) control the cellular ROS pool which in turn then drives the cells to their destined fate.

ABA signalling and PA metabolism was first provided by the seminal work of Toumi et al. [134]. This study provided evidence that differential ABA accumulation occurs in sensitive and tolerant cultivars of grapevine during drought stress. ABA induced the accumulation of PA and its exodus into the apoplast, where it got oxidized by the apoplastic amino oxidases (AOs) and produced H_2O_2 [134]. It also provided a functional link between PA and AO *via* ABA signalling for the regulated production of ROS which in turn signals for the execution of stress response or PCD. Link between PA, ABA and ROS is further supported by a recent report indicating exogenous application of Spermine – a tetra-amine, can protect soybean (*Glycine max*) seedlings from moderate osmotic stress induced by application of 9% polyethylene glycol (PEG) [135]. Spermine induced protection was found to be mediated by increase in ABA content along with increase in the activity of antioxidant enzymes that effectively reduce the cellular ROS pool elevated during osmotic stress [135].

The execution of both anhydrobiosis and PCD relies on very precise and successful modulation of ROS. Very low levels of ROS are maintained during anhydrobiosis while very high levels of ROS are allowed to be generated through oxidative burst during PCD. Interplay of ABA and Polyamines regulate both the processes by regulating ROS levels inside a cell. On certain instances, polyamines in combination with ABA are involved in surviving the drought conditions through the modulation of cellular ROS level [130,134,135]. For the execution of PCD the catabolism of polyamine is important. A brief overview of the underlying mechanism controlling anhydrobiosis and PCD is depicted in Fig. 1.

8. Conclusion and future perspectives

The observation of anhydrobiosis and PCD in plants is usually independent in occurrence. The faculty to sustain desiccation is prevalent in the amphibious and lower plants where water transport system is poorly developed or not developed at all. As during evolution these plants may have had faced frequent scarcity of water in their environment, they had adapted to suspend their metabolic functions in a reversible manner so that after arrival of favourable conditions normal functioning of the life can be resumed. As plants got adapted to terrestrial environments (higher plants) the anhydrobiotic capacity of plants was gradually lost from the vegetative phase and then became restricted to seed development, whereas the PCD processes gradually evolved to control developmental transitions and pathological scenarios. From regulatory point of view, both anhydrobiosis and PCD could be regulated by common growth regulatory plant hormones as elegantly exemplified by ABA – a well-known PCD promoting hormone under various stress conditions. ABA has also been shown to promote desiccation tolerance while negatively regulating PCD at the same time in barley aleurone cells [124,126]. Apart from ABA, polyamines have been shown to regulate PCD and anhydrobiosis by controlling the cellular ROS levels. This regulation and dual role of growth regulatory hormones in PCD and anhydrobiosis could be more widespread and general than currently anticipated. More studies looking into their contrasting roles need to be carried out to clarify and establish their roles. At the organism level, though both PCD and anhydrobiosis operate and are required for the plant survival but at the level of target cells or tissues the PCD and anhydrobiosis do not seem to operate simultaneously. For example, orthodox seeds show desiccation tolerance or anhydrobiosis in their maturation phase but PCD comes into operation when germination begins [124]. This observation suggests that there is some genetic switch that regulates which phenomenon to be operative at a given stage of the life-cycle of an organism. It leaves a fair possibility to explore and utilize the key regulators of anhydrobiosis and PCD for potential application in agriculture. It is interesting to note that none of cultivated crops represent anhydrobiosis at vegetative stage of their development [136]. For example, key regulators of vegetative desiccation-tolerance particularly from lower plants like bryophytes could be utilized to incorporate the same capacity in crop plants which either undergo PCD or do not sustain at all in the challenging and changing stress inducing environments.

Considering the important role that introduction of anhydrobiosis in crop plants may play in attaining global food security, focused and consistent research efforts are needed towards understanding the basic biology of anhydrobiosis in relation to PCD so that successful future endeavours can be taken to improve the yield of crops.

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